BIOLOGY OF THE GEOPHYTE, *TRITELEIA IXIOIDES* SUBSP. *ANILINA* (THEMIDACEAE), IN CONIFEROUS FORESTS OF BUTTE COUNTY, CALIFORNIA

Alfred Kannely
3558 Paseo Avenue, Live Oak, CA 95953
Alfred@ofir.DK

Robert A. Schlising
Department of Biological Sciences, California State University, Chico, CA 95929-0515

Abstract

The life cycle of the widespread, cormous geophyte, *Triteleia ixioides* (W. T. Aiton) Greene subsp. *anilina* (Greene) L. W. Lenz (Themidaceae) was studied in the field over several years in coniferous forest sites in Butte County, CA. All sites, ranging from 1383 to 1774 meters in elevation, have a Mediterranean climate and loamy soils above Tuscan mudflow substrate. Flowering scape height, corm weight, and corm depth varied significantly. Old corms decreased in dry weight throughout the winter, as shoots, roots, and new corms grew. By spring, each old corm had produced a leaf and a flowering scape, was depleted of stored food, and had a new "replacement corm" (without roots) already developed on top of it. Fruit set varied from 38.5% to 89.1%, with significant differences among populations sampled in different years and sites. Seed set was low (overall mean 38.4%), but varied significantly among years and sites, ranging from 26.4% to 56.3%. Plants are partially self-compatible. Soil moisture was not limiting to seed set, nor was pollen vectors, except on cold days. The most important pollinator was a bee fly (*Bombylius facialis*, Bombyliidae), although native bees provided some pollination at higher sites. Ten-minute observation periods, during bee fly activity, showed up to 15 visits to plants in a square meter. Percent seed germination was high (88–100%), with germination after the first rains and seedling growth continuing during the cold months. Seedlings produced single leaves up to 60.4 mm long, and corms averaged 1.6 ± 0.1 mm wide at one site. Contractile roots, produced lateral to the primary roots, averaged 16.13 ± 1.00 cm long. Shrinking and wrinkling at the upper part of the contractile root pulled the newly formed corm deeper in the soil. Study of contractile roots in *Triteleia* and other geophytes may help illustrate adaptation to summer drought in Mediterranean California.

Key Words: *Bombylius facialis*, contractile root, corm, geophyte, low seed set, scape-wasting, *Triteleia ixioides* subsp. *anilina*.

The geophyte is a very common growth form among perennial herbaceous plants in the region of California with Mediterranean climate. The term "geophyte" was defined by Raunkiaer (1934) for plants that die down yearly to an underground bulb, corm, or tuber at the end of one season and then renew growth from this organ when favorable growth conditions return. Although geophytes occur in many regions with different climates, Raunkiaer and others have long described them as especially adaptive in regions with Mediterranean and other summer-dry climates. In addition to drought avoidance, Pate and Dixon (1982) and Proches et al. (2005) concluded that a belowground "food storage function" was also of central importance in defining geophytes in the areas they studied.

In California a few recent studies on geophytes have focused on floral adaptations and pollinators (e.g., Dilley et al. 2000; Patterson and Givnish 2003). Several other studies have focused on belowground growth of the corm or bulb in California plants (Rimbach 1902; Smith 1930; Jernstedt 1984; Han 2001), some of which have dealt with the life cycle in relation to the summer drought of the Mediterranean climate (e.g., Tyler and Borchert 2002; Schlising and Chamberlain 2006). However, and importantly, in some accounts of California geophytes (Rundel 1996; Parsons 2000; Schlising and Chamberlain 2006) the authors noted there is a lack of basic information available on the field biology and complete life history for most members of the rich geophyte component in Mediterranean California.

Further investigation of individual species, and how they might differ from each other, will contribute to better understanding of the geophyte life form as a "strategy" in coping with predictable extremes inherent in Mediterranean climate. Such understanding may aid in long-term conservation of this important element of California's native flora.

Although not one of the seven taxa of *Triteleia* listed in the California Native Plant Society's Inventory of Rare and Endangered Plants of California (CNPS 2013), we chose to study *Triteleia ixioides* (W. T. Aiton) Greene (Themi-

daceae). It is an abundant and conspicuous geophytic component of open coniferous forests and meadow edges in our area (northern Sierra Nevada and southern Cascade Range). This species occurs from southwest Oregon to the Klamath and Cascade Ranges, the Sierra Nevada, and the Coast Ranges of California. Within this large geographic range, six subspecies are recognized (Hoover 1941; Lenz 1975, 1976; Pires and Keator 2012).

Very little information has been published on this species. Han (2001) investigated weights of corms in relation to scape and flower production when grown in cultivation and in the field. Berg (2003) described ovules and the embryology for *T. ixioides* flowers, but did not specify which subspecies was examined. Kannely (2005) reported the pollen: ovule ratio for *T. ixioides* subsp. *anilina* (Greene) L. W. Lenz, from one of the populations observed in detail in the present study.

The most recent morphological description (Pires and Keator 2012) for the subspecies we studied, *Triteleia ixioides* subsp. *anilina,* indicates that its spheroid corm produces one or two linear leaves 10–25 cm long and a flowering scape up to 30 cm tall when the leaves are drying. The umbel-like inflorescence has two to many yellow flowers with funnel-shaped tube and spreading lobes. The general habitat (Pires and Keator 2012) is conifer forest edges at 600–3000 m in elevation.

Since *T. ixioides* subsp. *anilina* occurs in the Klamath and Cascade Ranges, the Coast Ranges, and the Sierra Nevada (Pires and Keator 2012), our study in northern Butte County thus represents this subspecies near the center of its overall range. Apparently no field studies have been done that describe the field biology of *T. ixioides* subsp. *anilina.* Our study was done to provide basic information illustrating the phenology and life history of this common plant as it exists in forest habitats in northern Butte County.

Main goals were to 1) provide information on size of vegetative parts of the plants in relation to growth during different times of the year, 2) document flower visitors that might serve as pollinators, 3) determine the degree of reproductive success plants had in producing seeds, and 4) to investigate seed germination and seedling growth in relation to Mediterranean climate.

Study Area and Regional Climate

To incorporate potential variation in the study plants in northeastern Butte County three main study sites were used. These extended over about 25 km of coniferous forest habitat, and ranged from 1383 to 1774 m in elevation. Bedrock is Tuscan Formation volcanic mudflow, here representing the southernmost extent of the Cascade Range. Soils in major portions of all study sites

are rocky, and consist of sandy loam or loam, as determined with composite samples sent to A. and L. Analytical Laboratories, Inc., Memphis, TN. Current names for the specific soil types are not available, since the recent Soil Survey of the Butte County Area did not include this forested region.

All three study sites have a Mediterranean climate, with a shorter winter at the lowest site than at the other two. The lowest site has a weather-recording station nearby, approximately two kilometers southwest of Butte Meadows, at 1467 m elevation, for which 12 years of climatic measurements were available (www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?caCCRR accessed 12 April 2012). Climate data from this source were used to approximate conditions for all three sites, as no other climate data were available.

The lowest study site, "Ridge," is near a USGS benchmark at 1383 m elevation, on Carpenter Ridge, about 6.9 km southwest of Butte Meadows at 40°03′19.9″ latitude, 121°35′40.1″ longitude. Here, *Triteleia* plants grow mainly on the flat ridge top, and receive at least some shade every day during the growing season. Main forest trees are *Pinus ponderosa* Lawson & C. Lawson, *P. lambertiana* Douglas, *Pseudotsuga menziesii* (Mirb.) Franco, *Calocedrus decurrens* (Torr.) Florin, *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. and *Quercus kelloggii* Newb.; shrubs include *Ceanothus integerrimus* Hook. & Arn., *C. prostratus* Benth. and *Arctostaphylos patula* Greene. Herbaceous associates include *Penstemon neotericus* D. D. Keck, *Senecio aronicoides* DC., *Calochortus coeruleus* (Kellogg) S. Watson, *Allium campanulatum* S. Watson, *Kelloggia galioides* Torr., *Cordylanthus tenuis* A. Gray, *Mimulus torreyi* A. Gray, *Microsteris gracilis* (Douglas ex Hook.) Greene, and *Stipa stillmanii* Bol. Average annual precipitation (2000 through 2011) is 1211 mm from September through August (the Mediterranean rainfall year) with a low of 443 mm in the 2007–2008 study-year, and a high of 2160 mm in 2005–2006. Soil texture is sandy loam (71.3% sand, 21.1% silt and 7.5% clay) and is rockier than at the two other study sites.

The second site, "Meadow," is located 6.6 km east of Jonesville, and 0.32 km south of the road along Scotts John Creek, on U.S. Forest Service road 26N27, at 40°06′21.0″ latitude, 121°25′35.4″ longitude, and 1746 m elevation. *Triteleia* plants grow in bands between dense forest trees and a wet, sodden, three-lobed meadow. Here they receive shade from trees during much of the year. Trees are mostly *Abies concolor* and *Pinus jeffreyi* Balf.; shrubs include *Symphoricarpos mollis* Nutt. and *Ribes roezlii* Regel. Herbaceous associates are *Sidalcea glaucescens* Greene, *Hackelia californica* (A. Gray) I. M. Johnst., *Allium campanulatum, Mimulus torreyi, Dicentra uniflora*

Kellogg, and grasses such as *Elymus elymoides* (Raf.) Swezey subsp. *californicus* (J. G. Sm.) Barkworth, and *E. glaucus* Buckley. This site, 363 m higher than Ridge, has snow persisting longer. In all years of the study, snow on the local roads prevented spring observations until late May or early June. Soil texture is loam (50.8% sand, 35.4% silt and 13.7% clay).

The third (less intensively used) study site, "Creek," occurs 10.7 km east of Jonesville on Humbug Summit Road, adjacent to the California Department of Fish and Wildlife's Butte Creek House Ecological Reserve, at 40°05′16.8″ latitude, 121°24′59.2″ longitude, at 1774 m elevation. *Triteleia* occurs in openings and among sparse stands of *Pinus contorta* Douglas ex Loudon subsp. *murrayana* (Balf.) Critchf. and *Pinus jeffreyi*; the *Triteleia* plants receive at least some shade daily during the growing season. Associates include *Acmispon americanus* (Nutt.) Rydb., *Allium campanulatum, Mimulus torreyi,* and *Elymus elymoides* subsp. *californicus.* Being at the same approximate elevation, the climate here is similar to that of the Meadow site, as is the soil texture (loam, with 48.8% sand, 39.4% silt, 11.6% clay).

METHODS

Sampling Protocol

Populations were sampled similarly in most years from 2004 to 2009 from baselines (not starting at the exact same points), subjectively placed in areas with abundant *Triteleia* plants. Most parameters were measured on plants selected randomly along transects every 1–2 m, that were up to three m long and at right angles to the baselines. Additional transects were used to do destructive sampling, including collecting of corms and flower visitors, and to do experimental manipulations of flowers. Destruction of corms was limited to only several seasons so as to not significantly change the density of the plants in populations being studied. Specific features chosen for measurement were those that would characterize both vegetative growth and reproduction, and could be easily measured or assessed in the field.

Vegetative Features

Scape height was measured to the nearest 0.5 cm, from soil surface to base of the single umbellate inflorescence when plants were in fruit. Depth to the base of the corm was measured from the soil surface when plants were in fruit. To assess characteristics of the corms, harvested corms had their coats, shoots, and roots gently removed before corm diameters (width and height) were measured to the nearest 0.5 cm. Since corms were slightly flattened spheres,

volume was derived using the formula for an oblate sphere ($V_{oblate} = 4/3\pi a^2 b$). Corms were dried at about 37°C for one month to determine dry weight. Phenology and growth of new corms, and old corm replacement were studied in the field at Ridge, starting in September 2005 and ending in June 2006. Thirty plants in fruit were chosen randomly in September to have their corms harvested and measured. The four nearest plants (at the major compass directions from the harvested plant) were marked with wooden skewers in the soil, for comparative corm harvesting during the following months to show the nature of changes in the corms during the winter. In Meadow in 2007 plants with different degrees of symptoms of a "scape-wasting syndrome" were recorded in a 50 m² belt transect within the population that had been used for measurements and counts of various vegetative and reproductive features in preceding years.

Reproductive Features

Flowers. Flowers per plant were determined at time of fruiting, by counting the number of fruits and then adding the number of fruitless pedicels present (pedicels remain when flowers abscise). In order to characterize the mature adult portion of the population, only plants with two or more flowers were sampled. Pollen: ovule ratio was determined using the sonication method (Kannely 2005).

To determine if there was autonomous self-pollination, inflorescences at Ridge with flower buds ready to open were "bagged" using 15 by 20 cm lens paper (Fisher Scientific) closed at the base of the inflorescence with lightweight (Tot-50) staples. Space was left in the resulting "bag" for flowers to open completely; the "bag" was also secured to a wooden skewer pushed into the ground several cm from the scape. Entire inflorescences were harvested in five weeks. In 2007 this experiment was done with 32 plants, each paired with the closest control plant to the east, which was marked but not bagged.

Nectar was sampled at Creek in several flowers that had been bagged overnight, by using 10 μl micropipettes and a Bellingham and Stanley pocket refractometer reading 0–50% sucrose equivalents.

Quantification of insects visiting *Triteleia* flowers was done at Ridge in two seasons and at Meadow in one, by completing numerous 10-minute observation periods. One-meter square areas with six to 75 flowering plants were chosen subjectively to prevent spatial overlap. A standardized page with a large square representing a square meter of ground had all flowering plants quickly mapped, with the number open flowers written on each. The plot was watched for 10 min, and visits were recorded when an insect probed a

flower with its tongue. When an insect returned to probe a flower that it had probed even seconds earlier in the 10-minute period, this was recorded as another visit. A thermometer in the shade of the observer was read after 10 min. Thus, a record was made of flowers per plant, insect visits per plant, and how many plants were visited in sequence by a particular insect. Twelve specimens of the fly *Bombylius facialis* Cresson, were collected at Ridge on the morning of 29 June 2010 and were examined for pollen on their bodies.

Over three years 180 plots were watched (at Ridge, 70 in 2005, 40 in 2007 and 30 in 2008; at Meadow, 40 in 2005). In the three years a total of 2582 plants and 4281 flowers were observed. Isolated plants lying outside of the main transects of the study areas were not included.

Fruits and seeds. To assess the "success" of fruit and seed formation, number of fruits (and percent fruit set) per plant was determined just prior to dehiscence in July. Two mature fruits were collected, from opposite sides of each inflorescence, from plants along the main transects. These were put into separate #1 coin envelopes (Swinton Avenue Trading, Boca Raton, FL). In the laboratory each fruit was dissected to count mature seeds and ovules that had failed to become seeds, to determine ovules per ovary, seeds per fruit, and percent seed set. Seeds were counted as mature if they were black and had normal subspheric shape and size.

Seed weight, viability, and germination, and early seedling growth. Features of the seeds, including weight and viability, were determined using 200 black seeds collected from dehisced fruits, at Ridge and Meadow on 6 September 2005, and at Creek on 9 August 2008. In 2005 two Petri dishes had 50 seeds each from Ridge placed on filter paper, flooded with distilled water and kept in the dark for 45 hours. Seeds were cut in half, and placed with the cut surfaces facing downward in dishes of filter paper soaked with tetrazolium chloride. After 24 hours seeds were examined for staining of the embryos as indication of viability (Bradbeer 1988).

Timing of seed germination under field conditions was determined by planting sets of seeds collected from open fruits at the end of the season before fall rains began (Ridge, Meadow: 6 September 2005; Creek: 5 October 2008). Lots of 50 seeds each were spread along 20-cm strips of v-folded, non-inked newsprint (to permit finding seeds later), and covered with 8–10 mm of local soil. Rows were covered with squares of hardware cloth to help prevent disturbance by animals; seeds here received only natural precipitation. Rows of seeds and their supporting newsprint were recovered at intervals during the wet season and examined in the lab.

Data Analysis

One-Way ANOVAs and Tukey-Kramer comparisons were used on most plant parameters measured to determine if location and year were factors. When data did not meet assumptions for normality and equality of variances Kruskal-Wallis and Wilcoxen tests were compared with parametric tests. However, since we had reasonably large sample sizes, and the probabilities obtained from the non-parametric tests were nearly identical to the P-values obtained from the One-way ANOVA and Tukey-Kramer comparisons, we have reported the latter. Two-sample t-tests were used to compare means for corm diameters, seed weights, and length of seedling leaves. Most data were analyzed using Minitab 16 (Minitab Inc., State College, PA) and JMP PRO 10 (SAS Institute Inc., Cary, NC).

Results

Vegetative Features

General Morphology. Means for flowering scape heights were fairly uniform in the region, but scapes were significantly taller (P < 0.001) at the higher elevation site (Meadow) each year except 2007 (Fig. 1). The aboveground growth of scapes began approximately one month later in the spring at Meadow than at Ridge.

In 2007, an unidentified "scape-wasting syndrome" appeared on many of the plants interspersed among apparently healthy plants at Meadow. Of 169 scapes observed in a representative section of the population, only 12% of the plants appeared healthy, showing no apparent symptoms when observed on 22 June. The remaining plants showed symptoms, including whole scape upright, but with flowers dead (79%), or scape bent in the middle and with the inflorescence dying (9%). None of the plants with symptoms produced flowers that year. Several plants were noted with similar symptoms at Creek on 13 June 2007, but were not seen in any other year. *Triteleia* plants have also been found parasitized by a dodder (probably *Cuscuta californica* Hook. & Arn.) – one plant at Meadow in July 2006 and many plants at Creek in July 2008.

Corm depths (soil surface to base of corm) were significantly greater by three or more cm at Meadow than at Ridge both years measured (P < 0.001; Table 1). Corm volume did not vary significantly throughout the region, but corm dry weight was higher at Meadow (P = 0.01) (Table 1).

Small cormlets, vegetative side shoots produced by mature corms during spring growth, were rarely seen on corms dug at Ridge, but occurred more often at Meadow. At Meadow in
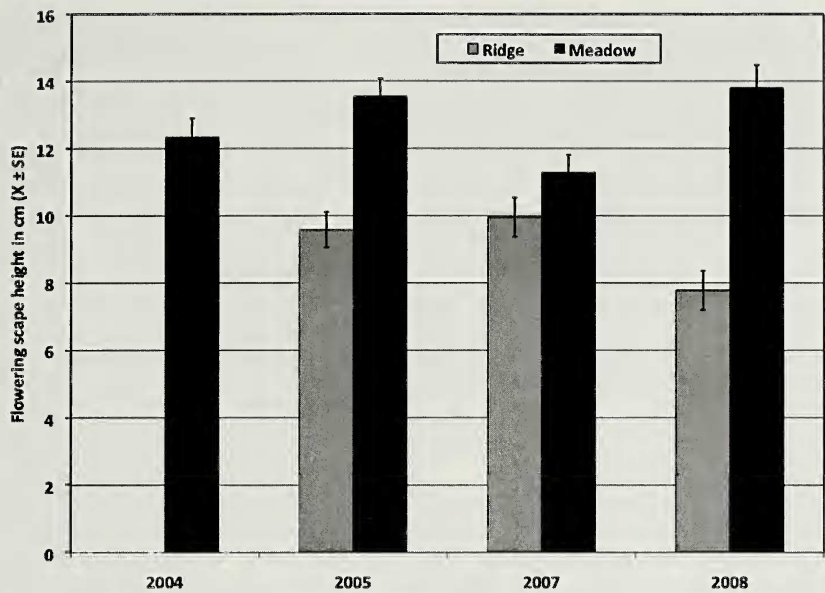
FIG. 1.   Flowering scape height in *Triteleia ixioides* subsp. *anilina* at two sites in Butte County. One-Way ANOVA with P = 0.0001 was followed by Tukey-Kramer comparisons, showing that scapes at Meadow were significantly taller than at Ridge, in each year except in 2007. Scape heights did not differ among the four years at Meadow except that they were significantly taller in 2008 than in 2007. Scapes at Ridge were shorter in 2008 than 2005. N was 30 in all samples, except 40 at Meadow in 2008, and 39 in 2007 and 41 in 2008 at Ridge.

2004, of 30 adult corms dug, 22 had between one and four cormlets. Cormlet dry weight (X ± SE) was 0.0256 ± 0.003 g (n = 45), compared with 0.259 ± 0.025 in the adult corms (Table 1).

Annual corm replacement. Corms that reached full size (Fig. 2a) at the time of fruit and seed maturation in June or July remained largely inactive until the fall/winter rains commenced. All of five corms dug 20 October 2005 at Ridge showed signs of renewed shoot (but not root) growth after 30.5 mm precipitation in the preceding weeks; shoot length above the flat upper surfaces of the corm was only 2–5 mm.

Corms sampled on 5 November 2005 (n = 25) after an additional 70.6 mm of rainfall, and again on 10 February 2006 (n = 24) showed an increase in shoot length and a decrease in corm weight (Fig. 3). Shoot length (cm) increased 357% (from 0.54 ± 0.027 to 2.47 ± 0.149), while corm weight (g) decreased 60% (0.208 ± 0.041 to 0.084 ± 0.012). In February these corms had numerous delicate roots which broke readily, several reaching up to 3.2 cm long. Heavy snowpack prevented sampling again until 5 May, by which time each old corm had produced a leaf (sheathing the shoot) that reached the soil surface. The single dark green leaf on the new shoot (n = 28) reached 5.88 ± 0.38 cm long, as measured from the ground surface. In addition, a new corm was obvious at the top of each old corm (Fig. 2b, top arrow). The weight of the old corms in May averaged less than in February but was still higher than the weight of new corms (0.035 ± 0.005 g vs. 0.009 ± 0.001 g; n = 23; P = 0.001). In May the growing scape (n = 28), visible

TABLE 1.   FEATURES (MEAN ± SE) OF CORMS IN *TRITELEIA IXIOIDES* SUBSP. *ANILINA* AT TWO SITES IN BUTTE COUNTY. Sample size is shown in parentheses (n). A t-test was used to compare corm volumes. One-Way ANOVAs were used for other parameters, with Tukey-Kramer comparisons used for means of corm depth and dry weight. In each column, means with the same superscript letters do not differ significantly.

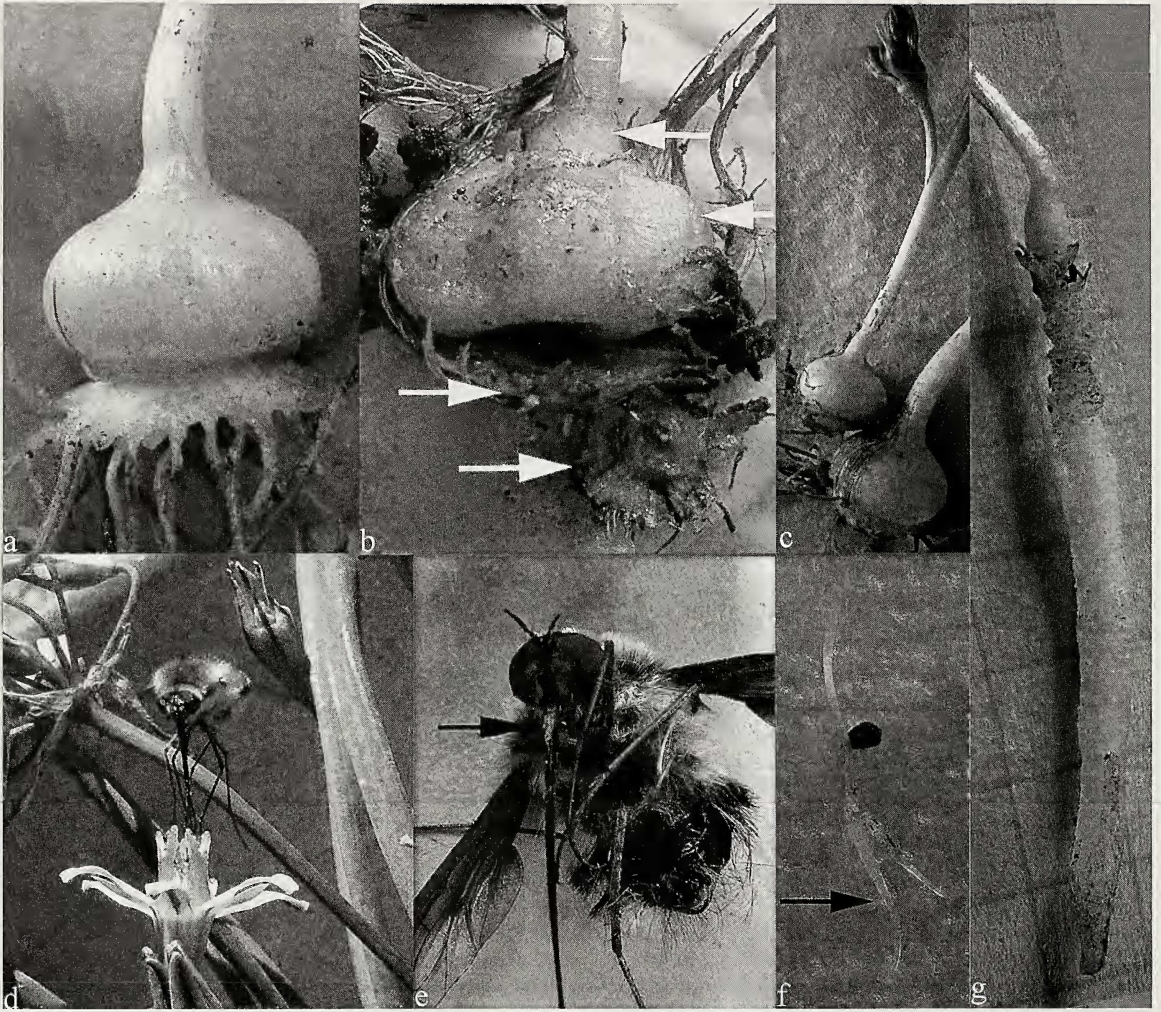| Site	Year	Diameter (cm)	Depth, from soil surface to base of corm (cm)	Volume (cm³)	Dry weight (mg)
Ridge	2005	0.98 ± 0.03[a]	5.03 ± 0.29[a]	0.39 ± 0.06[a]	0.168 ± 0.013[a]
	(n)	(30)	(30)	(30)	(31)
Meadow	2004	1.07 ± 0.04[a]	8.22 ± 0.6[b]	-	0.259 ± 0.025[b]
	(n)	(30)	(30)	(-)	(30)
	2005	1.01 ± 0.03[a]	9.31 ± 0.50[b]	0.41 ± 0.04[a]	0.236 ± 0.026[ab]
	(n)	(30)	(30)	(30)	(29)

FIG. 2. Features in the life cycle of *Triteleia ixioides* subsp. *anilina*. a. Rootless new corm (about 14 mm in diameter) in July, showing remains of earlier rooted corm. b. Multiple generations of corms, showing the youngest as a bulge (top arrow) at top of functional, rooted corm, and old and decaying remains of two earlier generations (bottom two arrows). c. Concurrent shoot and (white) new corm development in early June, growing from the functional, rooted old corm below. d. *Bombylius facialis* (head about four mm wide) probing a flower of *Triteleia*. e. Ventral view of *Bombylius*, showing *Triteleia* pollen at base of tongue. f. Seedling, showing primary and contractile (arrow) roots. Seed about three mm long. g. Seedling, near end of first year's growth, with small corm at the top of large contractile root. Gridlines at five mm.

within the sheathing leaf, averaged 2.86 ± 0.35 cm long.

When this study to characterize corm replacement ended on 8 June (Fig. 2c), the new corm (n = 29) was considerably larger and heavier (X = 0.140 g) than the depleted old corm (X = 0.014 g). The plants had flower buds on lengthening scapes, now at 7.68 ± 0.64 cm, but had leaves at final length (11.79 ± 0.49 cm). The new corms did not have any roots. By early summer old corms were shrunken and dried. In many plants there were also the still-older dried remains of a corm from earlier years visible (Fig. 2b, bottom two arrows).

Corms were heavily predated by pocket gophers (*Thermomys bottae* [Eydoux & Gervais, 1836]) most years at Meadow and Creek, but not at Ridge. Judging by tracks, black-tailed deer were responsible for many nipped scapes and leaves at all three sites. No insect damage was detected on vegetative parts.

Flowers and Fruits

Flower numbers and floral behavior. Numbers of flowers per plant from samples ranged from two to 27 (Table 2), with the overall mean for the 335 plants in the entire study being 8.2 ± 0.3.
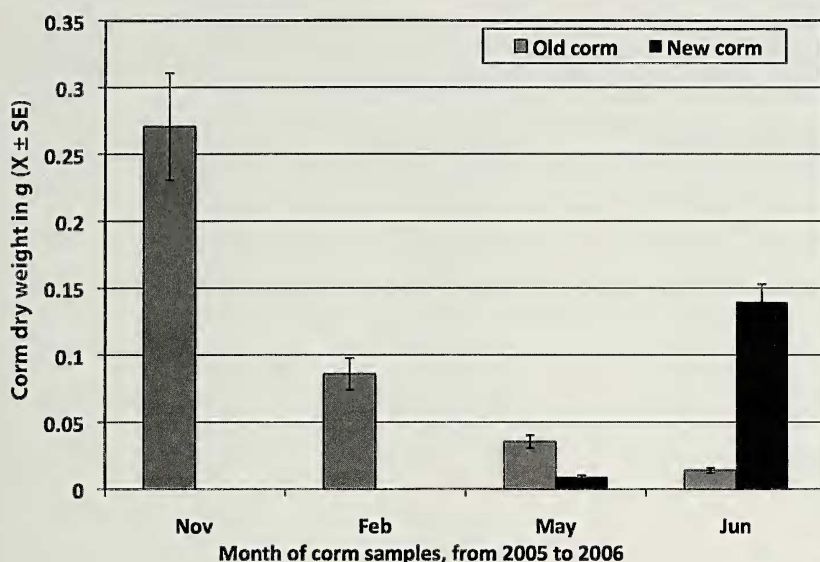
FIG. 3.   Corm dry weights in grams (X ± SE) for *Triteleia ixioides* subsp. *anilina* at Carpenter Ridge, from samples of neighboring individuals measured from 5 November 2005 to 8 June 2006. Old corms, producing the roots, leaf and flowering stem were depleted as aboveground growth continued during 2006. New corms, without roots, formed on top of the old, spent corms and permitted the plant to persist in a dormant state through the summer drought. One-way ANOVA (P = 0.0001) and Tukey-Kramer comparisons indicated that weights for *old* corms, November through May, were all significantly different from each other (P < 0.0001). *New* corm weight in June was significantly higher than in May (P < 0.0001). Sample sizes for the four harvests of corms were 25, 24, 28, and 29.

Flower number per plant was statistically higher at Meadow than at Ridge in 2005 and 2009, the two years when both sites were sampled (Table 2). The highest mean number of flowers per plant for all years was 11.2 ± 0.9 at Meadow in 2009.

Flowers opened by mid morning and remained open for 2–3 days. Anthers dehisced and stigmas appeared receptive at anthesis. Ovule number per ovary ranged from six to 22, depending on site and year (Table 3), but overall, mean number of ovules per ovary was generally consistent, with a mean value for all years of 12.9 ± 0.1 (n = 592). Mean ovules per ovary at Meadow was not significantly different in any of the five study years (Table 3).

The pollen : ovule ratio from 24 flower buds sampled at Meadow 25 June 2004 was 905:1 ± 70 (Kannely 2005), with 12,951 ± 1022 SE pollen grains per flower.

At Ridge in 2007, 97% of the plants (n = 32) with unbagged inflorescences set fruits, compared with (19%) that were bagged. Number of fruits per plant averaged 2.6 ± 0.24 in unbagged plants and 0.2 ± 0.09 in bagged plants.

Nectar production occurred simultaneously with anther dehiscence. This caused nectar samples to be easily contaminated with pollen and not suitable for a test. Nectar samples had to be combined to get a sufficient quantity to be measurable. Nectar from several flowers at Creek on 22 July 2006 read 35% sucrose equivalents.

Flower-visitors. Of the 4281 flowers observed in plots, 789 (18.4%) were visited by insects. A bee fly, *Bombylius facialis* (Cresson 1919) (Bombyliidae) (Fig. 2d, e) was the most frequent flower visitor; 721 (91.6%) of the visits were by this species. Other visitors included bumblebees (Apidae), solitary bees (including Megachilidae), syrphid flies (Syrphidae), an additional species of bee fly (Bombyliidae), and butterflies (Lycaenidae and Nymphalidae) (Appendix 1). Further quantification of insect visits to flowers is presented here only for *B. facialis*.

Numbers of *Bombylius* individuals that entered a single plot in 10 min ranged from zero to eight. Percentages of the plants in a single plot visited by at least one fly ranged from zero to 100%, with up to a maximum of 14 separate plants visited in sequence by a single fly that entered a plot, in 10 minutes (Fig. 4). Flies were usually scarce by mid-afternoon, probably due to depletion of the nectar in the flowers and/or very high air temperatures (e.g., 29–30°C). Flies were occasionally observed probing flowers of *Mimulus torreyi* or *Calyptridium monospermum* Greene, with flowers only about half as high off the ground as the *Triteleia* flowers, but nearly all the flies were seen only on *Triteleia* flowers.

Early in the season (e.g., at Ridge on 14–20 June 2005) there were few sightings of *Bombylius*

TABLE 2. COMPARISONS OF THE MEAN ± SE (RANGE) FOR NUMBER OF FLOWERS PER PLANT, FRUITS PER PLANT, AND % FRUIT SET IN *TRITELEIA IXIOIDES* SUBSP. *ANILINA* AT THREE SITES IN 2004–2009. A One-Way ANOVA indicating P = 0.000 for each parameter, was followed by Tukey-Kramer comparisons. In each column, means with the same superscript letters do not differ significantly.

Year	Site	n	Flowers per plant	Fruits per plant	% fruit set
2004	Meadow	26	7.2 ± 0.8[abcd] (2–18)	4.5 ± 0.5[ab] (0–13)	65.0 ± 4.5[ab] (0–100)
2005	Ridge	26	5.0 ± 0.4[d] (2–11)	3.6 ± 0.3[ab] (2–7)	73.8 ± 3.3[abcd] (40–100)
	Meadow	30	9.8 ± 1.1[abe] (2–26)	8.0 ± 0.9[cde] (2–22)	84.0 ± 3.3[cd] (30–100)
2006	Ridge	31	8.8 ± 0.8[abce] (3–27)	4.9 ± 0.4[abf] (2–12)	58.8 ± 3.5[b] (18.2–100)
2007	Ridge	32	7.1 ± 0.7[bcd] (2–19)	5.0 ± 0.5[abef] (0–16)	72.2 ± 3.6[abd] (0–100)
	Meadow	28	8.2 ± 0.7[abcde] (3–21)	6.0 ± 0.7[adef] (2–19)	71.9 ± 4.0[abd] (22.2–100)
2008	Ridge	33	5.4 ± 0.5[cd] (2–18)	2.2 ± 0.3[b] (0–7)	38.5 ± 4.8[e] (0–100)
	Meadow	32	8.7 ± 1.0[abcde] (2–22)	7.7 ± 0.9[cdef] (2–21)	89.1 ± 2.3[c] (50–100)
2009	Ridge	32	7.3 ± 0.5[abcd] (3–16)	4.8 ± 0.4[abf] (2–13)	66.6 ± 3.4[ab] (33.3–100)
	Meadow	30	11.2 ± 0.9[e] (4–21)	9.1 ± 0.9[c] (2–20)	79.1 ± 3.5[acd] (33.3–100)
	Creek	35	10.5 ± 0.9[ae] (3–26)	8.6 ± 0.8[cd] (2–22)	79.9 ± 2.5[acd] (43–100)

or other visitors); plot data from these dates are not illustrated. Most other days at both Ridge and Meadow had obvious active visitation by the flies. Percent of both plants and flowers visited by *Bombylius facialis* for these days is summarized by 1-hour periods at Ridge (Fig. 5) and at Meadow (Fig. 6). Additional data (including non-*Bombylius* visitors) for all plots covered in Figures 4–6 are shown in Appendix 1.

All bee flies collected had masses of pollen grains at the top of their non-retractable tongues (Fig. 2e), or elsewhere on the lower part of the head—positions that could contact a *Triteleia* stigma while a fly probed for nectar.

Features of fruits. Mean number of fruits per plant with one or more seeds for the entire study was 5.9 ± 0.2, but varied (Table 2) from zero to 22. In 2005, 2008, and 2009, three of the four years that Meadow and Ridge could be compared for fruits per plant, Meadow had statistically higher fruit set.

Mean % fruit set per plant was 71.1 ± 1.3 in the 335 plants examined in this study. Percent fruit set per plant ranged from zero to 100, but 2008 was the only year where Meadow had a significantly higher percent of the flowers forming fruits than did Ridge (Table 2). In recording phenological features of flowering and fruiting plants, we found that by early July at Ridge and late July at Meadow and Creek, scapes and leaves

were dead; fruits were mature and beginning to dehisce. As the summer progressed the fruit valves spread widely apart, permitting seeds to drop to the ground or to be flung out when scapes were moved by the wind or brushed by an animal. A few seeds remained in some fruits until fall. Dead scapes that did not get blown away or moved by animals stood into the winter if the snow was not deep, but under the weight of snow scapes were often pressed to the ground and were not visible by spring.

Numbers of mature seeds in the 592 fruits (from 296 plants counted in the six years of this study) ranged from 0–19 (Table 3), with an overall mean of 5.0 ± 0.1 seeds per fruit. Undeveloped ovules and seeds counted in sampled fruits indicated that reproductive success in terms of percent seed set, was low, with yearly means ranging from 26.4 to 56.3 (Table 3). The mean seed set combining all sites and years in this study was 38.4% ± 0.9%. No indication of predation on maturing seeds was found.

Seeds and Seedlings

Seed weight and viability. In 2005, *Triteleia* mean seed weight was higher (X ± SE) at Ridge (1.60 ± 0.03 mg) than at Meadow (1.24 ± 0.02 mg) (P = < 0.001; n = 200). Seeds collected 9 August 2008 at Creek averaged 1.23 ± 0.05 mg

TABLE 3. YEAR AND SITE COMPARISONS OF THE MEAN ± SE (RANGE) NUMBER OF OVULES PER OVARY, SEEDS PER FRUIT AND % SEED SET IN *TRITELEIA IXIOIDES* SUBSP. *ANILINA* AT THREE SITES IN 2004–2009. A One-Way ANOVA indicating P = 0.000 for each parameter, was followed by Tukey-Kramer comparisons. In each column, means with the same superscript letters do not differ significantly.

Year	Site	n	Ovules per ovary	Seeds per fruit	% seed set
2004	Meadow	24	13.3 ± 0.5[ab] (11–18)	4.5 ± 0.5[ab] (2–10)	33.3 ± 3.1[ab] (11.5–45.8)
2005	Ridge	26	11.9 ± 0.5[c] (6–17)	6.9 ± 0.6[c] (2–14)	56.3 ± 3.4[c] (22.7–91.3)
	Meadow	28	12.1 ± 0.5[bd] (7–16)	4.5 ± 0.4[ab] (0–8)	32.9 ± 2.7[ab] (0–62.5)
2006	Ridge	31	11.2 ± 0.5[d] (8–16)	4.7 ± 0.3[ab] (1–9)	42.3 ± 2.9[ad] (12.5–85.0)
2007	Ridge	32	13.0 ± 0.5[abd] (9–18)	6.8 ± 0.4[c] (3–13)	50.8 ± 2.2[cd] (26.3–80.0)
	Meadow	28	13.1 ± 0.5[abd] (6–18)	6.0 ± 0.7[a] (2–19)	26.4 ± 2.6[b] (8.3–58.6)
2008	Meadow	32	12.4 ± 0.3[bd] (9–16)	3.6 ± 0.2[a] (2–6)	28.9 ± 1.5[ab] (13–44)
2009	Ridge	32	14.5 ± 0.5[ac] (11–22)	6.8 ± 0.5[c] (2–14)	46.1 ± 3.0[cd] (18.2–86.7)
	Meadow	30	11.4 ± 0.4[bd] (7–16)	3.4 ± 0.3[a] (1–8)	30.0 ± 2.6[b] (5.6–64.3)
	Creek	32	16.0 ± 0.4[e] (12–22)	5.5 ± 0.3[bc] (3–9)	34.2 ± 1.5[ab] (18.8–53.0)

(n = 200). All embryos of the 100 Ridge seeds tested with tetrazolium chloride in 2005 stained bright red, implying high viability of seeds.

Seed germination and seedling growth. Recoveries from batches of 50 seeds on newsprint at all study sites indicated that 88 to 100% of the seeds germinated. Weather extremes and poor accessibility caused results to be spotty and incomplete for parts of this study (Table 4).

Time of germination and earliest seedling growth was documented only at Ridge in 2005–2006, since plantings at Meadow in 2005 (and at Meadow and Creek in 2008) were not accessible until late the following springs due to heavy snows. At Ridge, sprouts on seeds measured on 10 February (Table 4) showed that even at 1383 m elevation, *Triteleia ixioides* seeds had germinated and that seedlings were growing during the coldest period of the year.
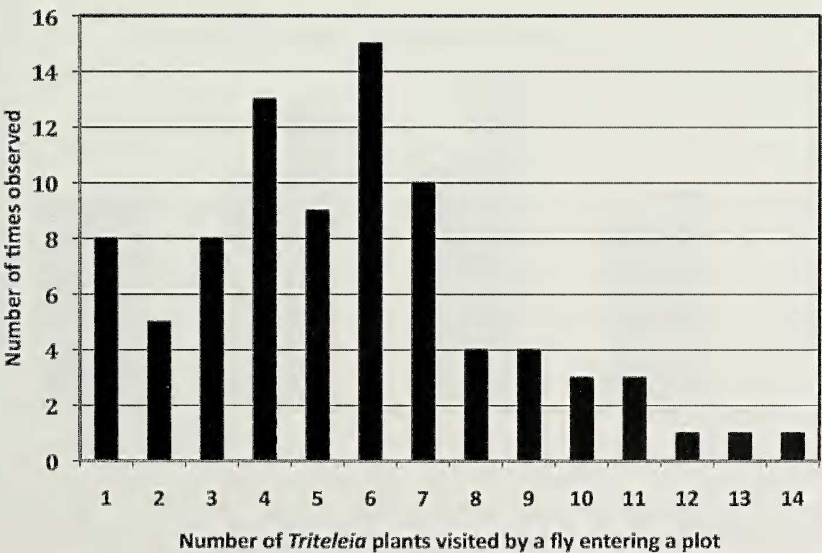

FIG. 4. Number of *Triteleia* plants visited in sequence by 85 individual *Bombylius* flies entering square-meter plots. Occurrences are combined from both sites and all dates shown in Figs. 5 and 6.
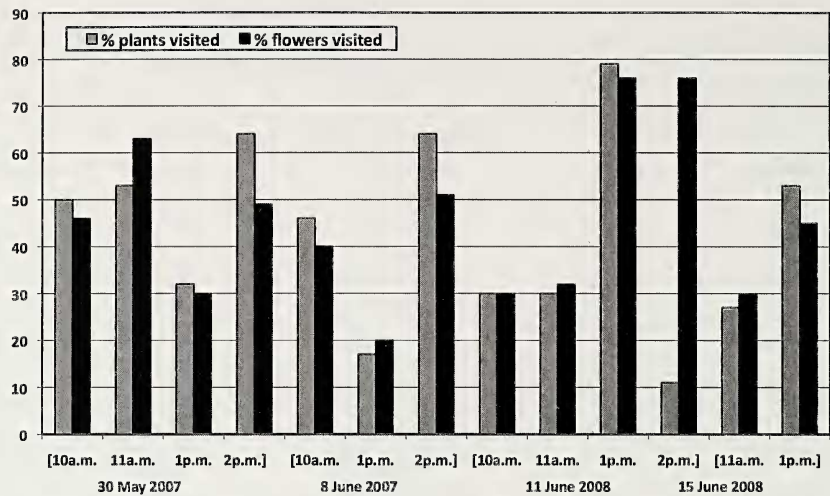
FIG. 5. Percent of *Triteleia* plants and flowers in plots at Ridge visited at least one time by *Bombylius facialis* in five consecutive 10-minute observation periods on dates when the flies were active. Note that dates for 2007 and 2008 are both included. The first 10-minute period started on the hour listed, but the other four periods in the hour started at slightly different times, as new plots were set up. Numbers of plants and flowers are shown in Appendix 1.

As sprouts grew, the tip of the cotyledon stayed in the seed, but the base of the cotyledon attached to the minute seedling axis often penetrated the newsprint. Later stages of growth in the spring months were sometimes inhibited by the newsprint, and only some, or portions of, seedlings could be reliably and accurately measured. For example, length of the first "true" leaf (arising on the shoot near the base of the cotyledon) was reliably measured in several instances, but length of seedling roots could be assessed well only one time (5 May 2006, in Table 4). On 5 May at Ridge all seedlings' green first leaves were visible above the soil surface.

Several of the seedlings at Ridge on 8 June 2009 showed initiation of the corm. There was a short region, up to 1.5 mm wide (wider than the base of the axis with the first leaf) that indicated early growth of the corm. More complete data were obtained at Creek on 28 June 2009. Here all seedlings were apparently near the end of first-year growth, with single leaves projecting above-ground and drying. First-year plants of *Triteleia ixioides* at Creek produced corms with mean
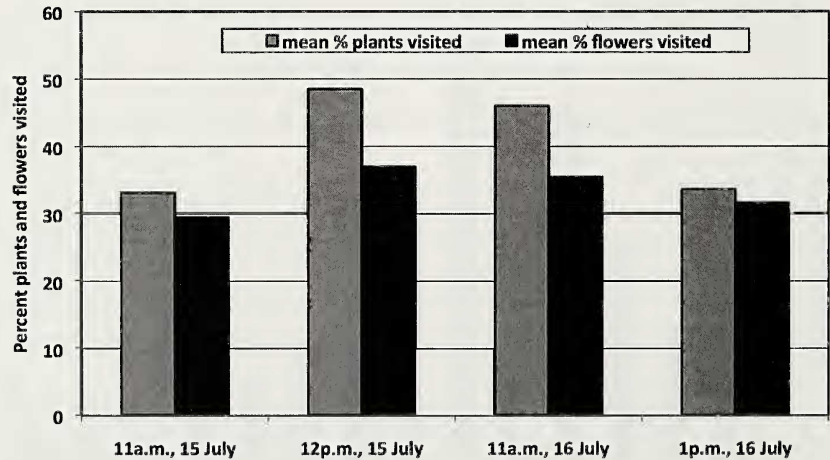
FIG. 6. Percent of *Triteleia* plants and flowers in plots at Meadow visited at least one time by *Bombylius facialis* in five consecutive 10-minute observation periods on dates when the flies were active in 2005. The first 10-minute period started on the hour listed, but the other four periods in the hour started at slightly different times, as new plots were set up. Data are shown as means from simultaneous observations by two people each hour. Although fewer plots were studied at Meadow than at Ridge (Fig. 5), these data illustrate the importance of *Bombylius facialis* at this higher elevation site. Numbers of plants and flowers are shown in Appendix 1.

Table 4. Selected Features of *Triteleia* Seed Germination and Seedlings, from Experimental Plantings. All length measurements are in mm, as X ± SE (n). The n (number of samples per planting) for % seeds germinated, lengths of sprout, first leaf, and contractile root may be fewer than the 50 seeds planted, due to loss or breakage. Mean length of first leaf of seedling on 8 June 2006 (from seeds planted 16 September 2005) was significantly longer at Ridge than at Meadow (P < 0.0001). For seedlings collected at Creek on 28 June 2009 leaves and roots were too desiccated or broken to provide accurate measurements, but mean diameter of first-year corms on these seedlings was 1.64 ± 0.075 mm. *Contraction wrinkling was seen in the proximal part of 28 of the 41 roots measured; primary roots were deteriorated. **A small swelling above top of root indicated start of corm formation in 45 of the 50 seedlings.

Study site	Date seeds planted	Date of seedling collection	% seeds germinated (n)	Length of "sprout" from seed coat (n)	Length of first leaf, from point of cotyledon attachment to the seed, to tip (n)	Length of contractile root from base of cotyledon (n)
Ridge	16 Sep 2005	10 Feb 2006	94 (47)	22.11 ± 2.17 (47)	- (-)	- (-)
		5 May 2006	100 (48)	- (-)	14.08 ± 0.83 (40)	16.13 ± 1.00* (41)
		8 June 2006	100 (48)	- (-)	48.4 ± 1.69[a] (43)	- (-)
Meadow	16 Sep 2005	8 June 2006	88 (44)	- (-)	15.7 ± 0.68[a] (42)	- (-)
Creek	5 Oct 2008	8 June 2009	100 (50)	- (-)	60.36 ± 1.51 (50)	9.94 ± 0.68** (50)
		28 June 2009	100 (39)	- (-)	- (-)	- (-)

diameters of 1.64 (±0.08 SE) mm before the young plants (n = 39) went dormant in the summer. Other plantings at Ridge and Meadow provided counts of seeds that germinated (Table 4), indicating 88 to 100% germination.

Seedlings were observed to have a contractile root. It appeared lateral to the primary root (Fig. 2f), at the base of the stem, where the corm forms. Figure 2g shows a large specimen, with the contractile root wider than the developing corm.

DISCUSSION

Growth of Plants During Different Times of the Year

Measurements of mature scape heights in different sites and years indicate there is variation in this aspect of growth (Fig. 1), as might be expected due to somewhat different microhabitats. Mature heights were reached just two to three weeks after the scape first appeared aboveground in May or June, and this occurred about a month earlier at the lowest elevation site (Ridge). We have also documented a "wasting syndrome" appearing in the scapes that heavily impaired reproduction in the Meadow population in 2007, but was not seen here in other years. Similar symptoms were reported for two populations of *Triteleia laxa* Benth. in grassland habitats in the northern Sacramento Valley in 1999 and 2001 (Schlising and Chamberlain 2006).

The cause of the symptoms or name of the disease has not been determined for either species, but these field observations illustrate a potential stress factor for *T. ixioides*.

Our field studies have shown that there is considerable subterranean growth in *T. ixioides* under natural conditions during the Mediterranean winter. Even with the low winter temperatures at 1383 meters elevation (or higher), considerable growth of the new corm occurs (Fig. 3). This represents an important variation in strategy when compared to herbaceous perennials that are winter-dormant.

We also illustrate how cormous geophytes like *T. ixioides* have plant bodies that last only a single year, since corms (Figs. 2–3) as well as aboveground parts are totally replaced each year. As the old rooted corm is expended producing a new shoot and flowers, a new rootless corm is being created before spring flowering is complete. This shows that provisioning for the survival of the individual plant body precedes reproduction by seed. New, rootless corms spend the late summer in a dormant state and begin to develop roots with the fall rains. Thus it appears that moisture availability may have a larger influence than temperature on breaking dormancy, a subject which may warrant further study.

Bee Flies as Pollinators of *Triteleia* Flowers

Our fieldwork provides a detailed example of a single species of bee fly as the primary pollinator

of *Triteleia ixioides* in Butte County. *Bombylius facialis* has been listed earlier, but without detail, as a pollinator of the vernal pool plant *Pogogyne abramsii* J. T. Howell in San Diego County (Schiller et al. 2000). Other published information on bee flies using California plants mentions the genus *Bombylius*, but does not provide numerical information on the fly visits (e.g., Grant and Grant 1965) or does not identify the specific *Bombylius* studied (e.g., Schmitt 1983). Our information comes from close examination in 1-m² plots over 110 separate 10-minute periods spread over different hours of the day (Figs. 4–6, Appendix 1). Thus we have obtained concrete, numerical documentation for a specific bee fly on a specific plant.

Adult flies in the Bombyliidae are thought to be pollinators while they collect nectar (Grant and Grant 1965; Kastinger and Weber 2001). Interestingly, Panov (2007) found that bombyliid flies (including several species of long-tongued *Bombylius* in Austria), also ingested large amounts of pollen through their tongues during short flower visits. A few studies in North America suggest that bombyliids may take in pollen as well as nectar, as from *Hedyotis* L. in New York (Grimaldi 1988) and *Commelina* L. and *Tradescantia* L. in Florida (Deyrup 1988). In *Triteleia,* nectaries are located in the three septa that separate the chambers of the ovary (see Vogel 1998 on the closely-related *T. lugens* Greene). Nectar secreted in the septa oozes out and drains through shallow channels to the base of the flower. While using pipettes to extract nectar, pollen was often found mixed in with it. This suggests that *Bombylius facialis* may have opportunity to ingest pollen in the nectar of *Triteleia* flowers.

When these flies probe flowers deeply with their extended tongues, abundant loose pollen accumulates on the base of the tongue and lower face (Fig. 2e); this pollen may brush onto stigmas during the probing, causing pollination. Our data show that in many cases a single fly may visit four to seven *Triteleia* plants (and less commonly up to 13 or 14 plants) in one square meter in just a 10-minute period (Fig. 4). Thus, they have great potential to significantly spread pollen among plants in a given population.

Bombylius facialis was seen as the most frequent flower-visitor beginning when ambient temperature was at least 20°C. This species of fly is considered common in the lower elevations of this region (Neal Evenhuis, personal communication). We have also observed this species at populations of *T. ixioides* subsp. *anilina* outside the study areas. However, we have evidence that along with *B. facialis*, bees and butterflies may also have importance as pollen vectors at the higher elevation sites such as Meadow (Appendix 1) and Creek.

Additional quantitative field study is needed to document variation in pollen vectors for *T. ixioides* and for other species of *Triteleia* that have wide geographic and/or elevational ranges. Flower color in taxa of *Triteleia* ranges from yellow to white, lavender and blue. The larger- and blue-flowered *T. laxa*, for example, observed at low elevations in the northern Sacramento Valley, was not visited by bombyliid flies, but rather by large butterflies and by bees (Chamberlain and Schlising 2008).

Reproductive Success, Based on Production of Fruits and Seeds

We have shown that reproductive success (based on fruit-set and seed set) varies between years and sites in our region (Tables 2 and 3). Definitive causes for this variation are not known, but could include pollen vector limitations and weather. Qualitative observations made during the flowering period suggested that soil water was not lacking. Our observations also show that pollen vectors are abundant, but only during warm weather. The short flowering period of *Triteleia,* along with temperature limitations of pollinators, suggests that vector activity does not always coincide favorably with flower receptivity to maximize seed set.

The presence of undeveloped white ovules along with mature black seeds in all 592 fruits examined shows consistent seed set below maximum potential. It is possible that low seed set (overall 38.4%) may be due to chromosomal anomalies, including polyploidy (as suggested by Lenz 1975). Lenz noted that for most populations of *T. ixioides* subsp. *anilina* he examined, plants had two sets of chromosomes ($2n = 14$); but he found one population in Sierra County where $2n = 42$. Furthermore, he noted that at meiosis chromosomes in the polyploids form rings or chains, and after division, daughter nuclei do not develop further. The relationship between low seed set and polyploidy warrants further investigation. Despite low overall seed set, nearly all fruits we sampled set some seed. Our bagging tests indicated that there is a degree of self-compatibility at the Ridge population, but we did not do tests using self-pollen. Although bagged plants were exposed only to self-pollen, it was not applied by hand.

Seed Germination and Seedling Growth in Relation to Mediterranean Climate

Seeds germinated at our lowest elevation site sometime after the first fall rains rather than in the spring, a phenomenon typical of many plants in Mediterranean areas. Seedling growth continued throughout the winter (Table 4) despite low air temperatures occurring at 1383 m elevation

(Ridge). Even with seasonal access difficulties, comparison of seedling morphology indicated that winter seed germination and seedling growth were similar at all three study sites. Harvesting batches of these seedlings at several times during their first year, permitted us to document the presence of contractile roots, which have also been described for *Triteleia hyacinthina* (Lindl.) Greene (Smith 1930, referred to as *Brodiaea lactea* (Lindl.) S. Watson; Pütz 1992) and *T. laxa* (Schlising and Chamberlain 2006). Since contractile root morphology and behavior is important in the context of plant growth under Mediterranean conditions, our documentation for *T. ixioides* warrants additional discussion of the scant literature here.

More than a century ago (Rimbach 1902) briefly described contractile roots as "subterranean organs" in several California "lilies" (e.g., *Scoliopus* Torr., *Trillium* L., *Zigadenus* Michx.) noting that such roots may function in pulling, to different degrees, young bulbs of seedlings downward in the soil from where they were first produced. Jernstedt (1984) described contractile roots in detail for *Chlorogalum pomeridianum* (DC.) Kunth, a large and widespread geophyte of Mediterranean California. She illustrated how the proximal (top) portion shrinks due to differential collapse and elongation in tiers of cells. The continued downward growth of the distal, growing portion of the root helps pull the bulb downward into the "channel" left by the shrinking root. Pütz (1996) also described the "pulling force" of contractile roots in some detail. Our outdoor plantings of *Triteleia ixioides* demonstrated fast-growing contractile roots lateral to the primary roots (Fig. 2f), but did not permit us to measure the extent that the shrinking of the roots moved the young seedlings' corms deeper in the soil. We found first-year contractile roots were significantly longer at Ridge than at Meadow (Table 4), perhaps because it was warm longer in the day, permitting more growth at the lower elevation.

The authors mentioned above who focused on California plants, described these roots in the context of the Mediterranean life cycle, and the fast "planting" of the seedling corm or bulb before the summer drought. Additional numerical information (Schlising, unpublished data) demonstrates contractile roots in seedlings, for species of *Brodiaea* Sm., *Calochortus* Pursh, *Dichelostemma* Kunth, and *Odontostomum* Torr. in northern California. Contractile roots on seedlings were emphasized by Rimbach (1902), but he also noted that contractile roots can be formed again on older plants in the years after the seedling stage. Pütz (1996) discussed the varying morphologies of contractile roots on both seedlings and older plants, and he noted that contractile roots are widespread geographically and occur in diverse habitats. In addition he illustrated this growth behavior as widespread in flowering plants in general – beyond the petaloid monocots that have been discussed here. An unusual example of eudicots with contractile roots in California was illustrated for *Jepsonia heterandra* Eastw. (Saxifragaceae) by Ornduff (1969).

Despite earlier work, contractile roots remain a poorly known plant feature. In the recent book "Seedling Ecology and Evolution" (Leck et al. 2008) such roots are not described as a feature of Mediterranean plants. Observations from our field study suggest that the "fast planting" by contractile roots in seedlings of *Triteleia ixioides* subsp. *anilina* may be a critical part of their adaptation to early summer drought in Mediterranean California. This may apply especially to the movement of the first-year corm to a somewhat safer, less-desiccating depth for over-summering during the dry season. More study is needed on contractile root ecology in general, especially as part of the life cycle of California geophytes.

Our field study has provided much information on life history and phenology for this species in nature. This is one of the two species of *Triteleia* for which much field information has been collected, with *T. laxa* being the other (Schlising and Chamberlain 2006; Chamberlain and Schlising 2008). It is hoped that our work provides a basis for continued study of not only this species but some of the rare *Triteleia* taxa, is a starting point for comparative studies on variations in strategy, and assists in conservation of California's geophytes.

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APPENDIX 1. NUMBER OF OPEN FLOWERS ON PLANTS OF *TRITELEIA IXIOIDES* SUBSP. *ANILINA*, WITHIN DIFFERENT ONE METER^2 PLOTS, AND QUANTIFICATION OF VISITS TO FLOWERS BY *BOMBYLIUS FACIALIS* DURING 10-MINUTE PERIODS AT RIDGE IN 2007 AND 2008 AND AT MEADOW IN 2005. Totals are sums for each of the five 10-minute periods done during the hour indicated. Visits by flies are listed separately for plot, plant, and flower. Percents (rounded) are given in parentheses. The last column lists other insects observed on *Triteleia* during the period (B = bumblebee, b = solitary bee, sy = syrphid fly, by = other bombyliid fly, lep = butterfly).

Site	Date	Start time for five consecutive 10-min observations (five different plots)	Plants with open flowers	Open flowers	Flies entering a plot	Maximum fly visits to a single plant	Total (and %) plants visited by at least one fly	Maximum plants visited in one sequence by a single fly	Total (and %) flowers visited by at least one fly	Other insects visiting flowers
Ridge	30 May 2007	10:00 a.m.	17	25	1	1	2 (10)	6	2 (0.1)	-
			12	14	6	4	10 (83)	8	12 (86)	-
			10	16	3	3	9 (90)	7	13 (81)	-
			11	15	2	1	4 (40)	3	4 (27)	-
			12	20	3	2	6 (50)	5	10 (50)	-
		11:00 a.m.	12	20	5	4	7 (60)	6	9 (45)	-
			10	28	5	4	8 (80)	7	17 (61)	-
			20	25	3	2	14 (70)	10	17 (68)	-
			18	25	2	2	14 (78)	11	15 (60)	-
			15	20	2	1	4 (27)	3	4 (20)	-
		1:00 p.m.	12	18	0	0	0	0	0	-
			23	34	0	0	0	0	0	-
			16	21	1	1	14 (88)	14	17 (91)	-
			18	26	0	0	0	0	0	-
			16	35	4	3	13 (81)	8	23 (66)	-
		2:00 p.m.	18	34	3	2	5 (28)	3	6 (33)	-
			18	28	6	3	16 (89)	9	23 (82)	-
			19	45	5	4	15 (79)	7	23 (51)	-
			13	21	5	4	13 (100)	9	17 (81)	by
			11	15	1	1	1 (9)	1	1 (7)	-
	8 June 2007	10:00 a.m.	10	15	1	0	6 (60)	6	7 (47)	-
			10	16	0	0	0	0	0	-
			16	23	2	1	7 (44)	5	8 (35)	-
			11	20	1	1	5 (46)	5	7 (35)	-
			20	22	2	2	13 (65)	13	14 (64)	-
		11:00 a.m.	13	16	0	0	0	0	0	-
			11	12	0	0	0	0	0	-
			13	19	0	0	0	0	0	-
			8	13	0	0	0	0	0	-
			10	15	0	0	0	0	0	-

APPENDIX 1. CONTINUED.

Site	Date	Start time for five consecutive 10-min observations (five different plots)	Plants with open flowers	Open flowers	Flies entering a plot	Maximum fly visits to a single plant	Total (and %) plants visited by at least one fly	Maximum plants visited in one sequence by a single fly	Total (and %) flowers visited by at least one fly	Other insects visiting flowers
		1:00 p.m.	15	20	0	0	0	0	0	–
			11	16	1	1	1 (9)	1	1 (6)	–
			13	25	2	2	9 (69)	7	17 (68)	–
			13	16	1	1	1 (8)	1	1 (6)	–
			14	17	0	0	0	0	0	b
		2:00 p.m.	15	20	1	1	6 (40)	6	6 (30)	–
			15	22	3	2	9 (60)	7	9 (41)	–
			13	21	2	2	13 (100)	11	16 (76)	–
			11	19	1	1	7 (64)	7	10 (91)	–
			19	34	1	1	12 (63)	12	18 (53)	–
	11 June 2008	10:00 a.m.	9	10	0	0	0	0	0	–
			7	8	0	0	0	0	0	–
			9	10	0	0	0	0	0	–
			10	11	1	1	3 (30)	3	3 (27)	–
			12	14	2	1	11 (92)	6	13 (86)	–
		11:00 a.m.	10	11	1	1	1 (10)	1	1 (9)	–
			14	16	1	2	9 (64)	10	12 (69)	–
			8	10	2	2	7 (88)	7	16 (80)	–
			14	18	0	0	0	0	0	–
			10	13	0	0	0	0	0	b
		1:00 p.m.	10	26	6	3	7 (70)	4	14 (54)	–
			14	23	1	1	7 (50)	7	14 (86)	–
			9	15	4	4	9 (100)	6	36 (44)	–
			15	19	2	2	14 (93)	11	16 (84)	–
			14	20	3	2	12 (86)	8	19 (75)	–
		2:00 p.m.	9	15	3	2	8 (89)	5	17 (93)	–
			9	9	8	4	9 (100)	4	19 (9)???	sy
			7	10	4	3	5 (71)	3	14 (71)	–
			7	10	0	0	0	0	0	–
			11	15	5	3	11 (100)	9	29 (93)	–
	15 June 2008	11:00 a.m.	7	9	0	0	0	0	0	–
			15	19	0	0	0	0	0	–
			8	10	2	1	3 (38)	3	4 (40)	–
			10	13	0	0	0	0	0	–
			12	16	2	2	11 (92)	8	16 (100)	–

APPENDIX 1. CONTINUED.

Site	Date	Start time for five consecutive 10-min observations (five different plots)	Plants with open flowers	Open flowers	Flies entering a plot	Maximum fly visits to a single plant	Total (and %) plants visited by at least one fly	Maximum plants visited in one sequence by a single fly	Total (and %) flowers visited by at least one fly	Other insects visiting flowers
		1:00 p.m.	10	17	3	2	7 (70)	5	12 (65)	-
			13	23	1	1	2 (15)	2	3 (13)	-
			9	13	0	0	0	0	0	-
			12	24	1	2	10 (83)	10	15 (63)	-
			13	21	3	2	11 (85)	6	14 (67)	b,by,lep
Meadow	15 July 2005	11:00 a.m.	8	12	4	3	5 (63)	4	8 (67)	-
			5	7	3	2	4 (80)	4	5 (71)	-
			9	18	3	2	5 (56)	3	8 (44)	b
			7	8	0	0	0	0	0	-
			15	20	0	0	0	0	0	-
		11:00 a.m. (2nd observer)	8	15	3	2	6 (75)	5	8 (53)	b
			11	14	1	1	1 (9)	1	1 (7)	-
			18	26	2	2	6 (33)	5	6 (23)	-
			15	19	1	1	7 (47)	7	8 (42)	-
			7	12	0	0	0	0	0	b
		12:00 p.m.	7	12	0	0	0	0	0	-
			9	12	2	2	5 (55)	5	6 (50)	b
			12	12	3	2	7 (58)	5	9 (75)	b,sy
			10	12	2	1	8 (80)	6	8 (67)	b,sy,lep
			9	12	3	2	6 (66)	4	7 (58)	b,b,lep
		12:00 p.m. (2nd observer)	12	22	1	1	4 (33)	4	5 (23)	b
			10	16	1	1	4 (40)	4	4 (25)	b
			13	20	2	1	6 (46)	4	6 (30)	b
			12	19	1	2	1 (8)	1	1 (5)	lep
			16	34	2	2	10 (63)	6	15 (44)	by
	16 July 2005	11:00 a.m.	13	15	2	2	6 (46)	4	8 (53)	-
			9	13	2	1	3 (33)	2	3 (23)	b
			14	16	4	1	6 (43)	2	6 (38)	-
			11	21	0	0	0	0	0	b
			10	25	2	1	2 (20)	1	3 (12)	b
		11:00 a.m. (2nd observer)	10	15	1	1	9 (90)	9	12 (80)	-
			6	6	3	3	5 (83)	4	5 (83)	-
			10	19	3	1	6 (60)	4	7 (37)	-
			8	11	0	0	0	0	0	-
			8	12	1	1	6 (75)	6	7 (58)	b

APPENDIX 1. CONTINUED.

Site	Date	Start time for five consecutive 10-min observations (five different plots)	Plants with open flowers	Open flowers	Flies entering a plot	Maximum fly visits to a single plant	Total (and %) plants visited by at least one fly	Maximum plants visited in one sequence by a single fly	Total (and %) flowers visited by at least one fly	Other insects visiting flowers
		1:00 p.m.	8	14	3	2	5 (63)	3	6 (43)	b
			11	16	1	1	4 (36)	4	6 (38)	lep
			14	25	1	1	4 (29)	4	7 (28)	-
			12	14	1	1	2 (14)	2	2 (14)	-
			11	18	0	0	0	0	0	lep
		1:00 p.m. (2nd observer)	13	20	2	2	7 (54)	6	12 (60)	b
			11	16	2	1	7 (64)	6	9 (56)	-
			14	23	2	2	10 (71)	6	14 (61)	-
			6	10	1	1	1 (17)	1	1 (10)	b,lep
			18	23	0	0	0	0	0	-